

The Pentastomes, *Waddycephalus teretiusculus* (Baird, 1862) Sambon, 1922 and *Parasambonia bridgesi* n. gen., n. sp., from the Lungs of the Australian Snake, *Pseudechis porphyriacus*¹

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(Text-figures 1-6)

INTRODUCTION

A FULL-GROWN SPECIMEN of *Pseudechis porphyriacus*, taken in Australia and purchased from a dealer, was received at the New York Zoological Park December 10, 1965, and died January 14, 1966. During this period it ate eight mice.

At autopsy, four large and 26 small pentastomes, all gravid females, were removed from the lungs. The pentastomes were killed and preserved in formalin. The large specimens, 45 to 50 mm. long, agreed in all particulars with descriptions of *Waddycephalus teretiusculus*, a species described originally by Baird (1862) as *Pentastomum teretiusculum* from the mouth of an Australian "copper-head" snake, *Hoplocephalus superbus* [*Denisonia superba*], which died in the gardens of the Zoological Society of London. A detailed anatomical study of the species was published by Spencer (1892) from material found in *Denisonia superba* taken on King Island, situated midway between the mainland of Victoria and Tasmania, and additional specimens that had been collected from the lungs of *P. porphyriacus* taken in Victoria. According to Spencer, the parasites were always firmly attached by their hooks with the heads buried deeply in the wall of the lung. A considerable pull was required to dislodge the creatures and

definite cavities were left. Spencer suggested that the specimen found by Baird in the mouth of the snake had migrated from the lung after the death of the host. Heymons (1935) stated that *W. teretiusculus* is widely distributed in Australia, and in addition to *D. superba* and *P. porphyriacus*, the parasite had been reported from the lungs of other Australian snakes: *Notechis scutatus*, *Demansia textilis*, and *Demansia psammophis*. Heymons (1941b) added that *W. teretiusculus* not only is common in Australian snakes but is parasitic in *Elaphe radiata*, a widely dispersed species that occurs in southern China, Bengal, the Malayan peninsula, Sumatra, and Java.

NEW MATERIAL

The present specimens are clearly members of the family Sambonidae Heymons, 1941, which comprises three genera: *Sambonia* Noc and Giglioli, 1922; *Waddycephalus* Sambon, 1922; and *Elenia* Heymons, 1932. The four larger individuals may be assigned positively to *Waddycephalus teretiusculus* (Baird, 1862). Indeed, Heymons' (1935, Fig. 1) drawing of the species might represent one of our specimens. These specimens are deposited in the American Museum of Natural History, No. 12927. The smaller individuals cannot be included in any of the described genera, and a new genus, *Parasambonia*, is erected to receive the new species that they represent. They are named *Parasambonia bridgesi*, in honor of William Bridges, for many years curator of publications and editor of *Zoologica*.

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Parasambonia n. gen.: Based on female only. Sambonidae; cephalothorax as wide as the abdomen; includes one or two cephalic annuli; sides of abdomen almost parallel; hooks simple, equal, median hooks slightly anterior to laterals; annulation often indistinct; lateral lines not apparent; about sixty annuli; uterine pore in sixth annulus from posterior end. Type species: *Parasambonia bridgesi* n. sp.

Differential diagnosis: *Sambonia* and *Elenia* are very similar; they are parasites of varanid lizards; the cephalothorax is small, much narrower than the abdomen, which is wide anteriorly and narrows to a stalklike posterior region; the hooks are very small, have a trapezoid arrangement with the anterior hooks somewhat larger than the posterior-lateral pair; lateral lines are recognizable. *Waddycephalus* is a parasite of Australian snakes, but it differs from *Parasambonia* in body form, gradually tapering posteriorly; the annulation is definite throughout with weak lateral lines; the hooks are unequal, the lateral pair smaller and anterior to the median ones. The most noteworthy difference between *Waddycephalus* and *Parasambonia* is the presence in the former genus of large glands, designated hook-glands by Spencer (1892), that extend along both sides of the intestine throughout most of the body.

Specific description, *Parasambonia bridgesi* n. sp.: The individuals of the smaller species were transferred to alcohol; twelve were stained in paracarmine or haematoxylin and mounted whole (Text-fig. 1); two were cut in transverse serial sections and stained with haematoxylin and erythrosin. The specimens are very uniform in size; they are slightly flattened ventrally and convex dorsally. They vary from 25 to 30 mm. in

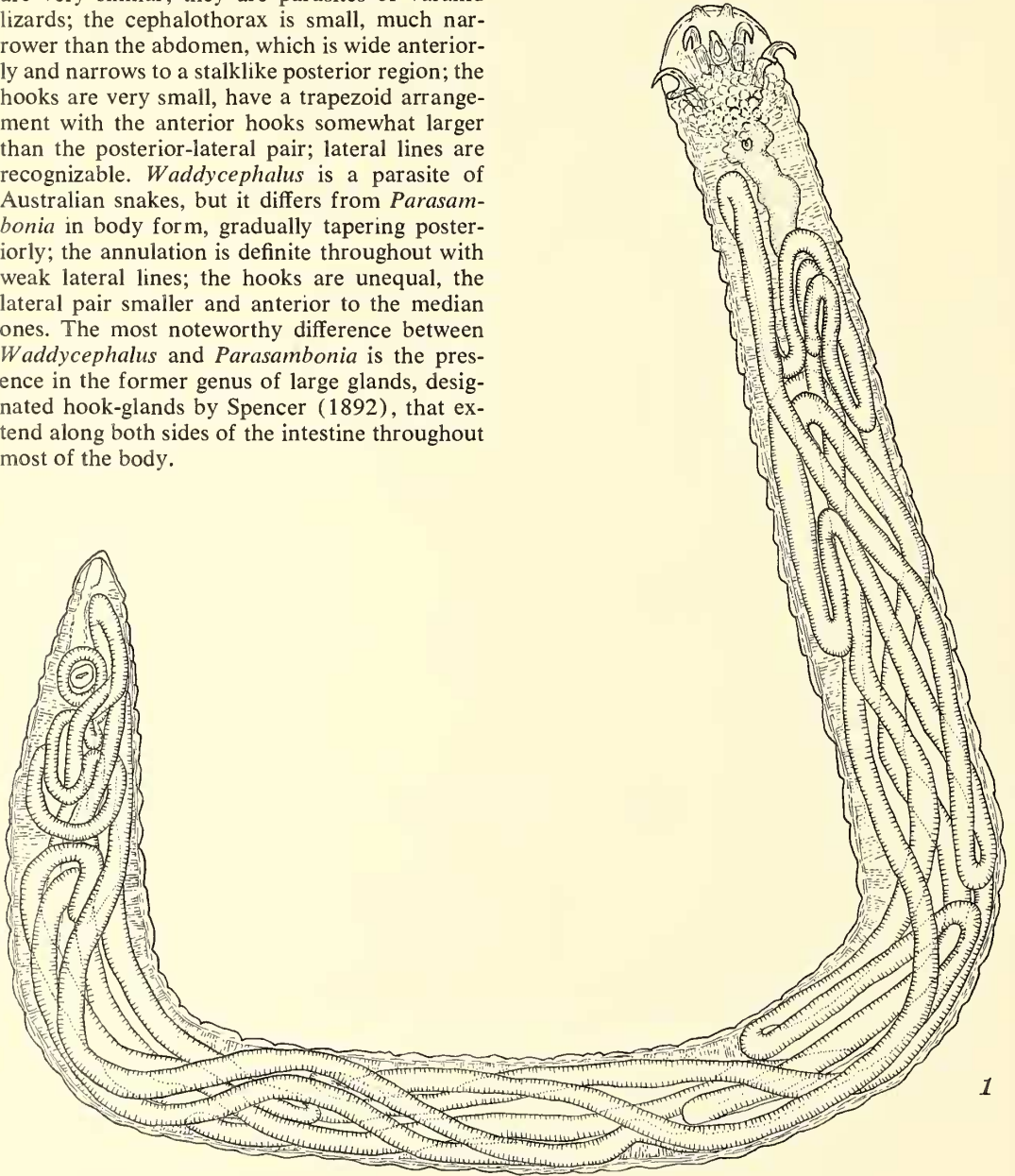


FIG. 1. Holotype, stained and mounted, ventral view, *Parasambonia bridgesi*.

length and 1.57 to 2.00 mm. in width. The abdomen is annulate but the annuli are often indistinct, especially at the posterior end and in regions where pressure from distended uterine loops obliterates the annulation. There is a slightly narrower region, comprising six to eight annuli, posterior to the cephalothorax and in the remainder of the abdomen, except for the caudal tip, the sides are almost parallel. The annuli in the anterior constricted region are about 1.57 mm. wide and 0.30 mm. long; throughout most of the body they are 1.65 to 1.90 mm. wide and 0.43 to 0.48 mm. long. In the specimen shown in Text-figure 1, the annulus that bears the uterine pore is 1.20 mm. wide and 0.25 mm. long. The posterior end of the body may be rounded or tapered to the tip. The terminal annulus has a slight dorsoventral cleft and the anus is located ventrally at the base of the cleft. As noted, in parts of the body the annuli are not distinct and in the region posterior to the uterine pore, 1.30 to 1.80 mm in length, the number could be determined in only two specimens. Although the total number could not be counted with certainty, there are about 60 annuli. Apparently the number varies slightly in different specimens.

No respiratory, circulatory, or excretory organs were recognized. The body cavity is a haemocoel; it contains a homogeneous fluid lacking cellular elements. Movement of the blood is effected by regional contractions of the general musculature. Throughout most of its length, the body cavity is occupied by loops of the uterus. Lateral lines, described for related species, were not observed. The cuticula measures 0.018 to 0.026 mm in thickness; it rests on a single layer of hypodermal cells. Scattered among the hypodermal cells on the dorsal and lateral sides of the head region, there are numerous, small, multicellular glands, the "Hautdrüsen" or "Stigmen-drüsen" of German authors. In addition, an irregular, staggered row of these glands (Text-fig. 2) extends around the annuli in most of the abdomen. They are often inconspicuous and apparently are absent near the posterior end of the body. In number and arrangement they are similar to those of *Sebekia oxycephala* as represented in Heymons (1935, Fig. 11). They vary from 0.030 to 0.045 mm. in diameter, with a transparent rim and a deeply staining core, some 0.010 mm. in diameter, which may be a central duct filled with secretion. These glands are bathed by the haemolymph of the body cavity and their function is still uncertain. The cuticula is turned in and lines the stomodeum, the procotodeum, the terminal portion of the uterus, and the pockets in which the hooks are located.

The cephalothorax is flattened ventrally and

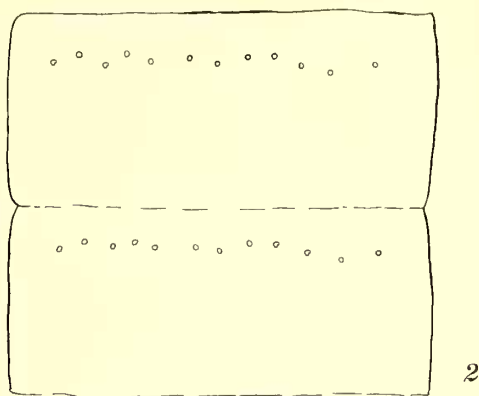


FIG. 2. Dermal glands on annuli, *Parasambonia bridgesi*.

from a lateral or ventral aspect, two annuli appear to be covered by or incorporated into it. It measures 1.60 to 1.90 mm. in width and 0.75 mm. to 1.20 mm. in length. The head is domed dorsally; the cuticula and hypodermis are separated from the underlying structures and the intervening region is large haemal sinus, which in fixed specimens is filled with a mass of coagulated body fluid. The anteroventral portion of the cephalothorax contains the muscular complex that operates the hooks. The hooks (Text-fig. 3) are simple, equal in shape and size, with the lateral hooks situated slightly posterior to the

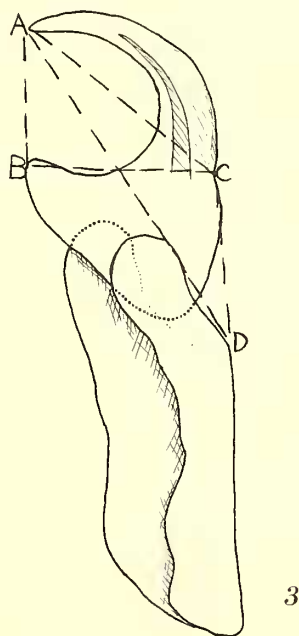


FIG. 3. Hook, *Parasambonia bridgesi*.

median ones. A scheme for measurements of the hooks was devised by Fain (1961). The measurements, as denoted in Text-figure 3, are: AB, 0.14 to 0.15 mm.; AC, 0.28 to 0.33 mm.; BC, 0.21 to 0.25 mm.; AD, 0.32 to 0.37 mm.; CD, 0.18 to 0.21 mm. The measurements AD and CD vary as the hook turns on the fulcrum. The fulcrum is 0.48 to 0.52 mm. long; it is concave ventrally, with two ventrolateral prongs that articulate on either side with the lateral base of the hook. Protractor muscles inserted on the hook at B and retractors inserted at C operate the rotary movements of the hook. Other muscles, inserted on the base of the hook and on the fulcrum, determine the position and orientation of the hook in the cephalothorax.

The anteroventral face of the cephalothorax bears two papillae, the "Tastpapillen" of Leuckart (1860), the "Sinnespapille A" of Haffner (1926) and the "Frontalpapillen" of Heymons (1935). They appear as protrusions of the body wall, anterior to and midway between the mouth and median hooks. In sections, they are pyriform, wider internally, 0.017 mm. long and 0.011 mm. wide, and resemble the "Papille A" of *Porocephalus clavatus* as figured by Haffner

(1926). The tip of the papilla bears a row of sensory cells, supplied by a nerve from the ganglion of that side, and contains the opening of a duct, 0.026 mm. in diameter, lined with low cuboidal epithelium, that extends dorsad and posteriad, lateral to the median sinus and above the musculature of the hooks. The duct appears to subdivide and terminate among the secretory cells located dorsal and lateral to the esophagus and the neural ganglia.

The paired ganglia (Text-fig. 4) are ventral, situated immediately posterior to the mouth. Each is 0.08 to 0.09 mm. in lateral and 0.06 to 0.07 mm. in dorsoventral measurements, and a commissure from the anterior part of the ganglia passes dorsally around the esophagus. Paired nerves extend from the ganglia to cephalic structures and a principal midventral pair extends posteriad through the length of the body. In the dorsolateral region, posterior to the esophagus and anterior to the intestine there are masses of secretory cells, each 0.06 to 0.08 mm. in diameter, with nuclei that measure 0.016 to 0.02 mm. in diameter and contain nucleoli that stain deeply. These cells appear comparable to the "Kopfdrüsen," "Frontal-

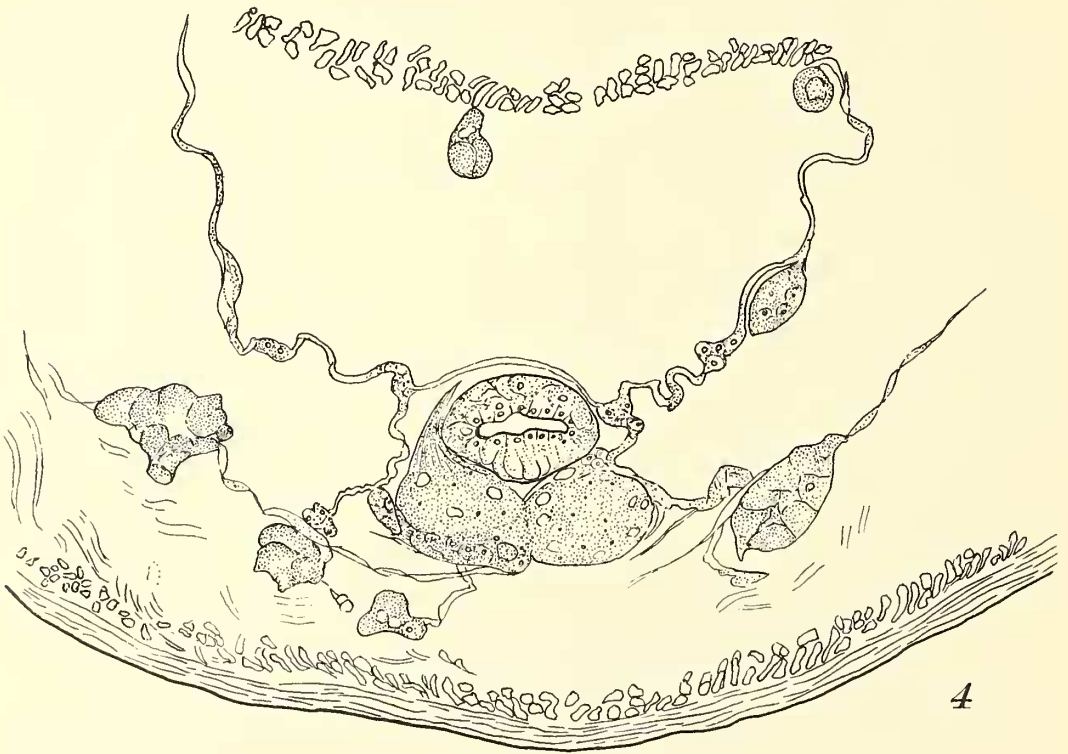


FIG. 4. Cross section through the subesophageal ganglia, *Parasambonia bridgesi*.

drüsen," or "Hakendrüsen" of Heymons (1935) and other authors. The function of these glands is problematical and the same is true of the so-called "Parietaldrüsen," occasional small groups of glandular cells situated along the abdomen between the somatic musculature and the body wall.

The mouth is situated between the median hooks, 0.50 to 0.60 mm. from the anterior end of the body. It is oval, longer in the anteroposterior axis; the opening varies from 0.08 by 0.16 to 0.12 by 0.23 mm. The mouth is situated in a cuticular frame, (Text-fig. 5), 0.41 to 0.48 mm. long and 0.21 to 0.25 mm. in greatest width. The pharynx, dorsal to the mouth and the esophagus, lined with cuticula, extends posteriorly above the ganglia to open into the intestine in the third or fourth annulus. The intestine is straight, leading to the anus at the posterior end of the body, but the wall of the gut has many large, internal folds (Text-fig. 6).

The ovary is a flattened tubular structure with lateral wings. It is supported by a mesentery and applied to the dorsal surface of the intestine. It begins a short distance anterior to the uterine pore, near the level of the middle of the metraterm, and extends to the fourth annulus from the anterior end of the body. Here paired oviducts pass ventrad on either side of the body and join in a wide tubular structure that receives ducts from the two seminal receptacles. The receptacles are oval, 0.60 to 0.75 mm. long and 0.45 to 0.54 mm. wide. They are situated on opposite sides of the body and may

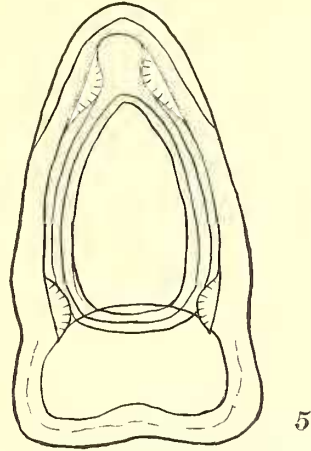


FIG. 5. Circumoral cuticular frame, *Parasambonia bridgesi*.

be at the same level or one may be anterior to the other. After fertilization, the eggs pass into the uterus. The uterus has a thin membranous wall and is disposed in many loops (Text-figs. 1, 6). The uterine pore is situated on the ventral surface of the sixth annulus from the posterior end of the body. The terminal portion of the uterus, comparable to the metraterm of the digenetic trematodes, is constricted, has a strong muscular wall consisting of outer circular and inner longitudinal fibers, and has a cuticular lining. It extends anteriorly from the uterine pore for 0.70 to 0.80 mm., where it becomes continuous with the last thin-walled

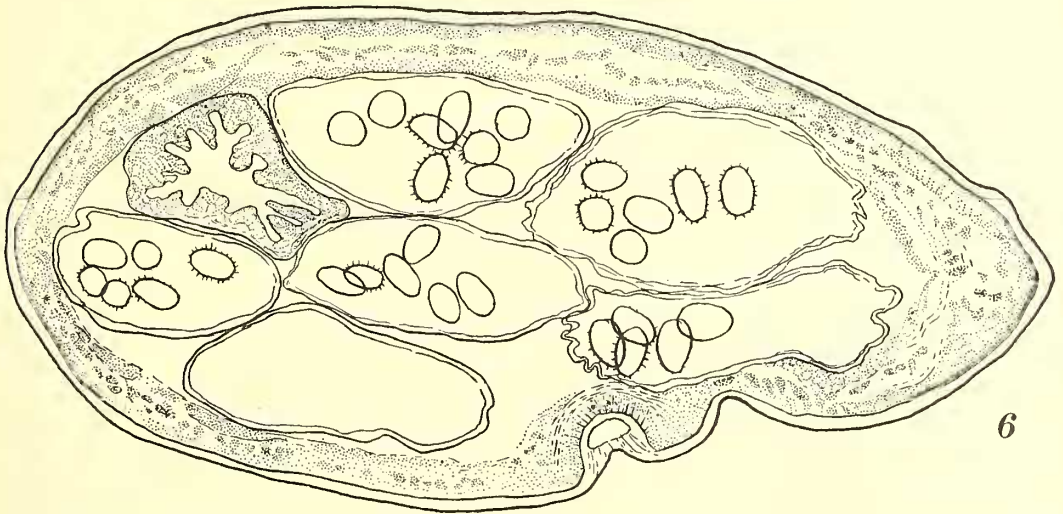


FIG. 6. Cross section through the uterine pore, showing eggs, uterine coils at this level, and folded wall of the intestine, *Parasambonia bridgesi*.

loop of the uterus, which turns posteriad to the level of the pore and then crosses to the opposite side of the body, where it loops posteriad. Newly formed eggs are oval, have smooth shells, are remarkably uniform in size, and average 0.055 by 0.038 mm. The shells of older eggs (Text-fig. 6) are 0.074 by 0.052 mm. and are covered by cylindrical projections, 0.005 to 0.007 mm. long, which appear to be embedded in a transparent matrix with a delicate membranous covering. Eggs in the terminal portion of the uterus contain fully formed larvae.

Type depositary: American Museum of Natural History, holotype No. 12924; paratypes: whole mounts and sections No. 12925; specimens in alcohol, 12926.

DISCUSSION

The first comprehensive study of the morphology and life cycle of the pentastomes was made by Leuckart (1860). He demonstrated that *Pentastomum denticulatum* (Rudolphi, 1809) Rudolphi, 1819, is the larval stage of *Pentastomum taenioides* (Rudolphi, 1809) Rudolphi, 1819, and that both are identical with *Linguatulida serrata* Fröhlich, 1789. In a footnote, Leuckart (1860, p. 2), noted that several helminthologists, including von Nordmann and van Beneden, had employed the generic name *Linguatula* Fröhlich, 1789, which he conceded was correct and in accord with the law of priority. But, influenced by the prestige of Rudolphi, German investigators had assigned species to the genus *Pentastomum* Rudolphi, 1819, and since the majority of named species had been described as members of *Pentastomum*, Leuckart adopted the name, although it is a junior synonym of *Linguatula*.

Classification: The classification of the pentastomes is based largely on the work of Sambon and Heymons, with a revision by Fain (1961). In early literature the tongue-worms, as they were called, were included in the family Linguatulidae and comprised three genera: *Linguatula* Fröhlich, 1789, *Porocephalus* Humboldt, 1809, and *Pentastoma* Rudolphi, 1819. In a contribution published in two parts, Sambon (1922a, June 15; 1922b, December 15) made extensive additions to knowledge of these parasites. He (1922a) divided the family Linguatulidae into two subfamilies: Raillietiellinae, based on *Raillietiella* Sambon, 1910, and Porocephalinae n. subf., based on *Porocephalus* Humboldt, 1809. The genus *Linguatula* was placed in the subfamily Porocephalinae, an obvious error, since it was the nomenclatural type of the family and must be type of the subfamily to which it is assigned. The two subfamilies

recognized by Sambon are morphologically distinct, and Sambon noted that in the Raillietiellinae the hooks are borne on stumplike protrusions of the body wall; the female genital pore is near the anterior end of the abdomen; the uterus is straight and sacciform; and the larva has six short, stumpy legs. In the subfamily Porocephalinae, on the other hand, the hooks are sessile; the female genital pore is at or near the posterior end of the body; the uterus is tubular, elongate, with numerous windings; and the larva has four legs. Sambon transferred several species to *Raillietiella* and included the genus *Reighardia* Ward, 1899, in the subfamily Raillietiellinae. The Porocephalinae were divided into three sections: I. Sebekini, with the genera *Sebekia* Sambon, 1922; *Alofia* Giglioli, 1922; and *Leiperia* Sambon, 1922; II. Porocephalini with the genera *Porocephalus* Humboldt, 1809; *Kiricephalus* Sambon, 1922; *Armillifer* Sambon, 1922; and *Wadycephalus* Sambon, 1922; III. Linguatulini with the genera *Linguatula* Fröhlich, 1789, and *Subtriquetra* Sambon, 1922.

Noc and Giglioli (1922) erected the genus *Sambonia* to contain *Pentastomum clavatum* Lohrmann, 1889, a species that had been included in the genus *Sebekia* by Sambon (1922a). In a paper published on October 27, Heymons (1922) described *Raillietiella mabuiae* and erected a new genus, *Cephalobaena*, to receive a new species, described as *Cephalobaena tetrapoda*, taken from South American snakes. He included *Cephalobaena* and *Raillietiella* in a new family, Cephalobaenidae. But *Raillietiella* had been named as a type of the subfamily Raillietiellinae by Sambon (1922a), and since the name of the family and type subfamily must be formed from the name of the type genus, the family name must be Raillietiellidae, and Cephalobaenidae is a subjective synonym. Sambon (1922b) suppressed *Cephalobaena* as a synonym of *Raillietiella*, discussed previously described species, and compiled a list of the Linguatulidae, arranged according to classification, definitive hosts, and geographical distribution.

Heymons (1935) published a comprehensive treatise on the Pentastomida and presented a revised system of classification. The group was accorded the taxonomic status of a class. He noted that the two names, Pentastomida and Linguatulida, were equally available; and although *Linguatula* antedates *Pentastoma*, he chose to follow Leuckart and adopted Pentastomida as the name for the class, because Rudolphi had formulated a concept of the group, whereas Fröhlich merely described a larva

from the lungs of the hare. Rudolphi's concept of the group was vague, however, since he included *Pentastomum* in the Trematoda, between *Polystomum* and *Tristomum* on the mistaken belief that the hooks of the pentastomes were comparable to the suckers and hooks of the pectobothriid trematodes, which at the time were believed to be anterior in position. Comparison with other invertebrate groups led Heymons to the conclusion that the pentastomes were derived from annelidlike progenitors; moreover, their morphology and distribution suggested an isolated and phylogenetically ancient group, probably parasitic in extinct paleozoic reptiles. In a recent study, Osche (1963) reaffirmed the arthropod affinities of the pentastomes.

In the class Pentastomida, Heymons (1935) recognized two orders: Cephalobaenida, with two families, Cephalobaenidae and Reighardiidae; and Porocephalida, with two families, Porocephalidae and Linguatulidae. Since suprafamilial names are not subject to the rules that apply to family names, the order Cephalobaenida is acceptable, but as noted earlier, if *Raillietiella* and *Cephalobaena* are in the same subfamily, the name of the family must be Raillietiellidae. The family Reighardiidae contained only the genus *Reighardia*. In the family Porocephalidae, Heymons recognized four subfamilies: I. Porocephalinae with five genera; *Porocephalus* Humboldt, 1809; *Armillifer* Sambon, 1922; *Kiricephalus* Sambon, 1922; *Waddycephalus* Sambon, 1922; and *Ligamifer* Heymons, 1932. II. Sebekinae with three genera; *Sebekia* Sambon, 1922; *Leiperia* Sambon, 1922; and *Alofia* Giglioni, 1922. III. Diesinginae with two genera; *Diesingia* Sambon, 1922; and *Elenia* Heymons, 1932. IV. Samboninae, new subfamily, to receive *Sambonia* Noc and Giglioni, 1922. The family Linguatulidae contained two genera: *Linguatula* Fröhlich, 1789, and *Subtriquetra* Sambon, 1922. The two orders recognized by Heymons are virtually identical with the two subfamilies of Sambon (1922a). Heymons (1940) noted the agreement between *Sambonia* and *Elenia* and suggested that the two may be identical. In a later report, Heymons (1941a, p. 323) stated "Die drei Gattungen, *Sambonia*, *Elenia* und *Waddycephalus* stehen einander sehr nahe." Further comparison led to the conclusion that the two genera, *Sambonia* and *Elenia* should be retained and four genera, *Sambonia*, *Elenia*, *Waddycephalus*, and *Ligamifer*, were characterized. The subfamily Samboninae was elevated to family status to contain the first three genera. Relationship of *Ligamifer* to the genus *Armillifer* was noted

with the comment (Heymons, 1941a, p. 325), "Wo der Trennungsstrich zwischen Sambodiden und Armilliferiden zu ziehen ist, wissen wir noch nicht."

In a revision, Fain (1961) retained the two orders Cephalobaenida and Porocephalida. Cephalobaenida contained two families: Cephalobaenidae and Reighardiidae. The Cephalobaenidae contained three genera: *Cephalobaena* with a single species; *Raillietiella* with 19 species arranged in five groups; and *Megadrepanoides* Self and Kuntz, 1957, with two species. The order Porocephalida was divided into two suborders: Porocephaloidea and Linguatuloidea. The Linguatuloidea contained the single family Linguatulidae and the single genus *Linguatula*. The suborder Porocephaloidea contained five families: Porocephalidae, Sebekidae, Armilliferidae, Sambonidae, and Subtriquetridae, a new family, to receive the genus *Subtriquetra*, which was transferred from the Linguatulidae. The family Sambonidae contained three genera: *Sambonia*, *Elenia*, and *Waddycephalus*. Fain noted that infection by two different species of pentastomes is a rare occurrence. It is interesting also to note that with the exception of two genera—*Reighardia*, whose only species occurs in birds; and *Linguatula*, with species only in mammals—all other pentastomes are parasites of reptiles. Larval stages occur in fishes and mammals, but specimens become adult only in amniotes.

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